

Successful and Unsuccessful Predation of the Gastropod *Nucella lapillus* (Muricidae) on the Mussel *Mytilus edulis* from Maine

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Abstract. The behavioral components of prey selection of the muricid gastropod *Nucella lapillus* (Linnaeus, 1758) were reconstructed from 546 large (25–100 mm anteroposterior length), drilled valves of the blue mussel *Mytilus edulis* Linnaeus, 1758, collected from Sand Piper Beach, Appledore Island, Maine. Regression of outer borehole diameter on prey valve length indicates that muricids were selective of prey size, although the degree of correlation ($r^2 = 0.117$) is lower than for smaller size (< 35 mm) classes of mussels reported in the literature, indicating a relaxation of size selectivity by the predator in larger mussel size classes. The rare occurrence of boreholes in mussels up to 100 mm in length suggests that the relatively thin shell (~ 3 mm) of even large mussels alone was not an effective defense against drilling predators. Prey effectiveness in deterring drilling predators, indexed by the ratio of unsuccessful drilling attempts to the total number of attempted drillholes, increased as mussel valve length increased, suggesting a higher probability of interruption of the drilling process by abiotic or biotic factors later in ontogeny. Twenty-nine percent of boreholes initiated by the predator were either incomplete ($n = 151$) or repaired ($n = 97$) shortly after the drilling process was completed. In contrast to previously published results, drillholes are not preferentially clustered on the dorsal umbonal and posterodorsal portions of the valve. Cryptic placement of boreholes on the thicker ventral region of the valve may have reduced the risk of detection of the driller by other foraging predators during the prolonged drilling process of large mussels (> 4 days).

INTRODUCTION

The blue mussel *Mytilus edulis* Linnaeus, 1758 is a moderately large, epibyssate bivalve that is common along western Atlantic shorelines, attached to rocky substrates. A common predator of *M. edulis* is the intertidal to shallow subtidal muricid gastropod *Nucella lapillus* (Linnaeus, 1758), which drills a cylindrical hole through the mussel's shell (Figure 1) (see Carriker, 1969, 1981; Carriker & Van Zandt 1972; and Carriker & Williams 1978 for discussions of the drilling process). The stereotypic components of prey size- and drillhole site-selection by dogwhelks feeding on intertidal mussels have also been studied extensively under both field and experimental conditions (Seed, 1969; Palmer, 1983, 1984; Hughes & Dunkin, 1984a, b; Burrows & Hughes, 1989; Hughes & Drewett, 1985; Hughes et al., 1992; Hunt & Scheibling, 1998).

Previous studies have concentrated on the predator-prey interaction among small upper shore populations of *M. edulis* (< 40 mm shell anteroposterior [A–P] length). But blue mussels may occasionally reach lengths in excess of 100 mm (Stanley, 1970). It is reasonable to suspect that blue mussels may attain a valve length or thickness late in ontogeny that cannot be successfully handled by drilling muricids. Consequently, large and thickened valves of adult mussels may serve as effective morphological defenses against drilling gastropods, as in other

co-occurring predator-prey interactions (Vermeij, 1978; Palmer, 1983; Norberg & Tedengren, 1995; Elner, 1978; Hughes & Elner, 1979; Leonard et al., 1999).

Drilling events are also not invariably successful (Figure 1A–F, K, L). Most studies have focused on successful drilling events and have not quantified the frequency of unsuccessful events. Incomplete boreholes are relatively common in muricid-mussel interactions (Vermeij, 1982; Seed, 1969) and represent either an interruption of the drilling process or a limit (thickness) to prey handling of the predator. The probability of interruption is proportional to drilling time (Hughes & Dunkin, 1984a); thus, large, thicker-shelled mussels may have accumulated multiple unsuccessful drillholes as the thickness (i.e., handling time) of the shell increased throughout ontogeny. Mussels have also been reported to repair boreholes that perforated the shell (Figure 1A, C–F, L) (Seed, 1969; Griffiths & Blaine, 1994). Seed (1969:337), working with the *Mytilus-Nucella* interaction, stated that, “where the whelk has been disturbed before doing any serious damage, the mussel can seal off the hole by means of a pearly concretion secreted by the mantle.” It is not known, however, how frequently these repaired boreholes occur or in what size classes of *M. edulis*.

This study reconstructs the foraging behavior of *N. lapillus* feeding on large mussels when the preferred smaller prey size classes are rare or absent. Alternative predatory

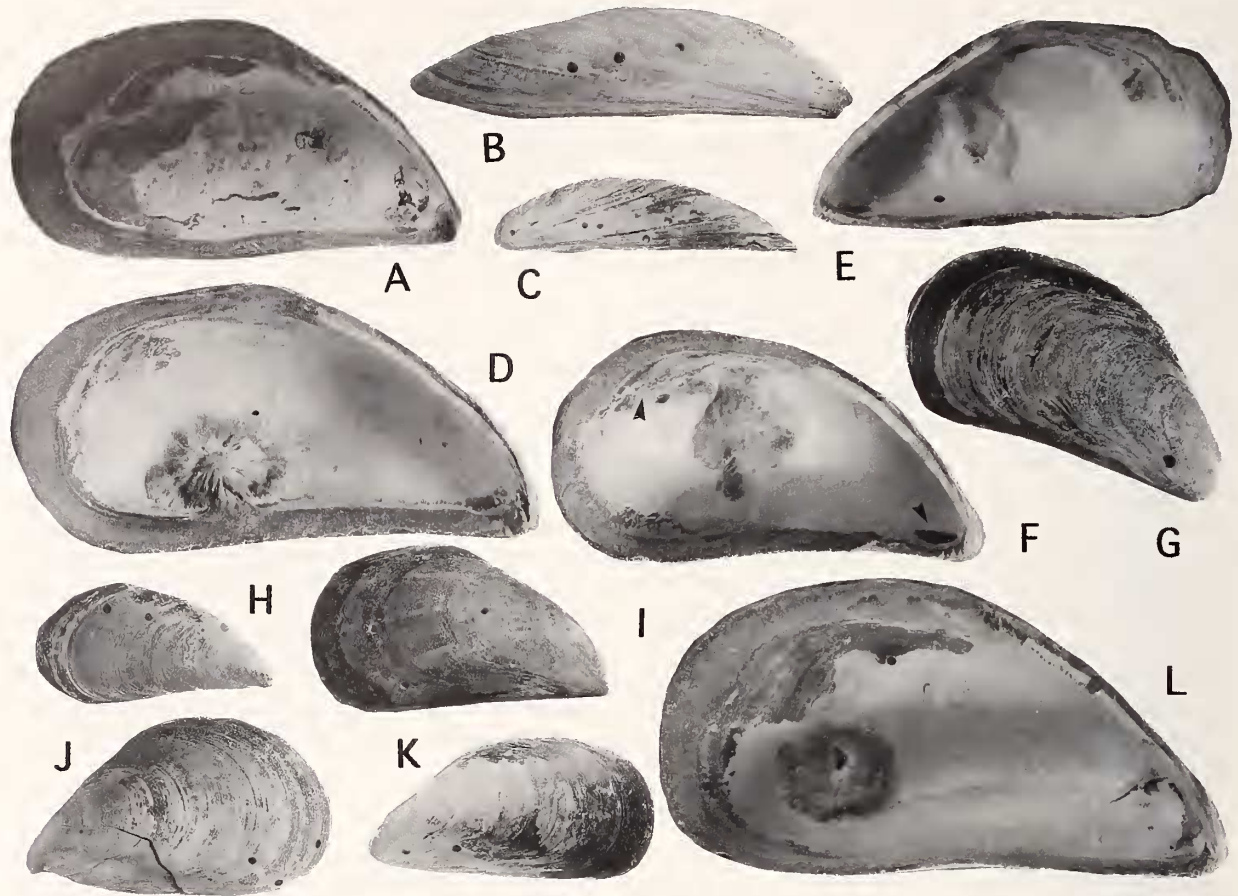


Figure 1

Predatory drillholes in valves of *Mytilus edulis*. A. Interior view of a valve with a blisterlike repaired borehole. The borehole penetrated the valve in the umbonal region of the shell. $\times 1.0$. B. Multiply drilled ventral portion of a valve; the posteriormost drillholes are repaired, and the anterior borehole is incomplete. $\times 0.8$. C. Anterior-most drillhole is incomplete, the next two are repaired, and the last three are complete. $\times 0.8$. D. Large blister in ventral portion of valve. Note complete borehole along the dorsal periphery of the repair. $\times 1.0$. E. Repaired drillhole in the dorsal portion of the valve and a more ventrally located complete borehole. $\times 1.1$. F. Repaired drillhole. Note positions of anterior and posterior adductor muscle insertion (arrows) showing the absence of a nacreous shell layer. $\times 1.0$. G. An oversized complete borehole in the ventral-umbonal sector. $\times 1.0$. H. Multiple drillholes in the dorsal portion of the valve. Note location of the anteriormost drillhole along the dorsal valve edge. $\times 0.6$. I. Valve with four complete boreholes. Note the two juxtaposed ventral boreholes. $\times 0.6$. J. Three complete drillholes located in posteroventral region of the valve. Two of these drillholes are close to the valve edge. $\times 0.7$. K. Anterior-most drillhole is incomplete and the other is complete. $\times 0.7$. L. Interior view of a valve with two repaired drillholes. The anteriormost repair has flaked off, artificially producing a complete borehole. $\times 1.0$.

strategies that exploit large prey with increased handling times are discussed and contrasted to predicted patterns of selective predation established under experimental conditions.

MATERIALS AND METHODS

Drilled valves of the mussel *M. edulis* were collected from a gravelly, shelly, high intertidal lag deposit on Sand Piper Beach, on the wave-protected side of Appledore

Island, Maine. This sample affords the unique opportunity to investigate the predator-prey relationship between adult dogwhelks (> 25 mm in shell height; Hughes et al., 1992) and large *M. edulis* (> 35 mm A-P length); this relationship has not been quantified in the literature. Hunt & Scheibling (1998) reported that the outer diameter of the borehole (OBD) is positively related ($r^2 = 0.986$) to the height (H) of the shell of *N. lapillus* by the regression equation, $OBD \text{ (mm)} = 0.135 \times H \text{ (mm)}^{0.576}$. This equa-

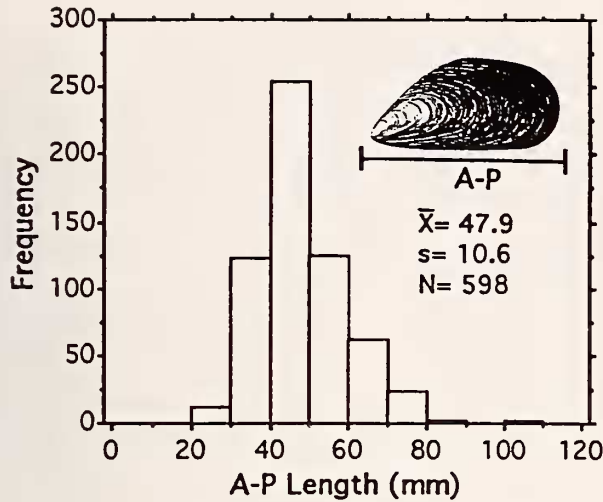


Figure 2

Size frequency distribution of anteroposterior (A-P) lengths of the valve of *Mytilus edulis* with complete boreholes.

tion predicts that adult *N. lapillus* greater than 30 mm in shell height drill boreholes greater than 1.0 mm in diameter. In this study, approximately 96% of complete drillholes have OBDs greater than 1.0 mm.

The size-frequency distribution of valves of *M. edulis* with complete drillholes (Figure 2) suggests that this death assemblage was most likely a low-shore subtidal population of mussels. Even though smaller size classes (< 25 mm A-P length) may have been selectively winnowed by currents, most low-shore subtidal populations of mussels are predominantly composed of only large mussels (Seed, 1969). Seed (1980) also stated that in low-shore habitats, sheltered from wave action, growth rates may be enhanced, resulting in increased size of mussels. Moreover, brachyuran crabs may influence the local distribution and population structure of their mytilid prey, in low-shore and subtidal habitats, by preying selectively upon small mussels (Kitching et al., 1959; Ebling et al., 1964; Seed, 1990).

Shell size was determined by measuring valve A-P length and dorsoventral height using Vernier calipers to the nearest 0.05 mm on 546 left and right valves of *M. edulis*. Both OBD and inner borehole diameter (IBD) were measured with a micrometer-calibrated binocular microscope. Outer borehole diameter and IBD are both reliable correlates of predator size (Carrier & Van Zandt, 1972; Hunt & Scheibling, 1998; Palmer, 1988). In order to evaluate selectivity of prey size, principal components analysis was used to describe covariation between the dimensions of the borehole (predator size) and dimensions of the mussel valve (prey size) (Table 1). In addition, to facilitate comparisons with data on juvenile to subadult dogwhelk-mussel interactions (Hunt & Scheibling, 1998), OBD was regressed on mussel length to determine the

Table 1

Principal component analysis of the correlation matrix of dimensions of predator (OBD and IBD) and prey (Length and Height).

Eigenvectors	1	2	3	4
Length	0.56	-0.43	0.00	-0.71
Height	0.57	-0.42	-0.11	0.70
OBD	0.46	0.52	0.72	0.05
IBD	0.39	0.61	-0.69	-0.06
Eigenvalues	2.24	1.43	0.27	0.06
Explained Variance	56.0	35.7	6.8	1.5

flexibility (or amount of variation) in prey selection for different size classes of the predator (Figure 3).

Seed (1969) and Hughes & Dunkin (1984a) have reported that *N. lapillus* commonly drills the dorsal regions in valves of *M. edulis* from exposed shores. Accordingly, the site of each complete drillhole was assigned to one of six sectors in a grid superimposed on the valve surface (Figure 4). The null hypothesis that all sectors were drilled equally was tested using a Chi-square goodness-of-fit test (Figure 5). Expected frequencies of boreholes in a sector were calculated to be proportional to the average surface area of each sector.

In this study, unsuccessful drilling attempts were sorted into two groups: (1) incomplete drillholes and (2) drillholes that perforated the shell but were later repaired by the mussel (Figure 1D, F, L). A Chi-square goodness-of-fit test determined if unsuccessful drillholes (incomplete

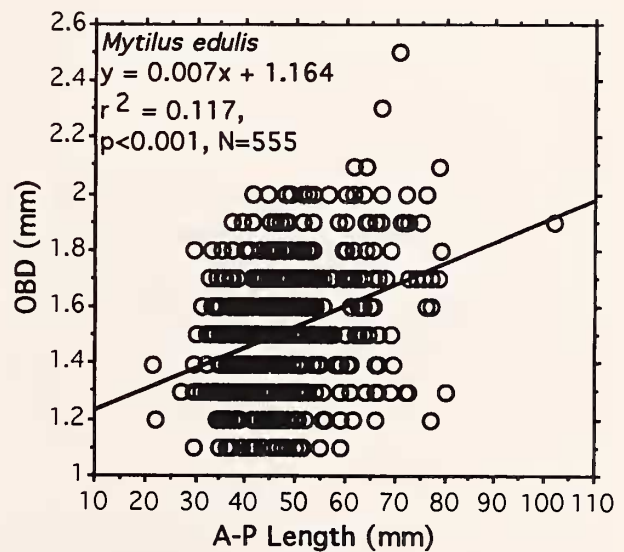


Figure 3

Regression of outer borehole diameter of complete boreholes (OBD > 1.0 mm) on mussel anteroposterior (A-P) length for the sample of *Mytilus edulis* from Maine.

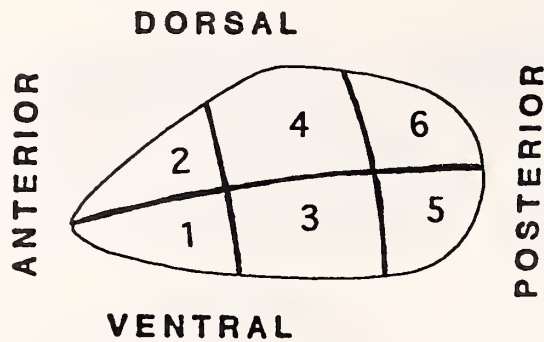


Figure 4

Sector grid used to determine site location of the drillhole.

and repaired types treated separately) were distributed among the six sectors of the valve in proportion to the observed frequency of complete drillholes for each sector (Table 2). Any differences in observed versus expected frequencies, of successful and unsuccessful drilling attempts, may reflect the extent of postero-anterior shifts of unsuccessful boreholes with post-drilling shell accretion. Higher observed relative to expected frequencies of unsuccessful drilling events in umbonal sectors (1–2) and lower than predicted observed frequencies in more central and posterior sectors (3–6) would suggest that postero-anterior shifts in borehole positions had occurred.

A Poisson distribution was fit to the observed frequencies of boreholes for each group and a goodness-of-fit test (G-test) used to determine if the occurrence of a borehole on a valve was independent of the occurrence of other boreholes for multiply drilled valves (Table 3). A significant result would suggest that the probability of the occurrence of successive boreholes on a valve was not independent of the first drillhole. Poisson distributed data reflect the chance that the occurrence of multiple complete, incomplete, or repaired boreholes in any one valve is very small.

Prey effectiveness (PE), the probability that an individual survives in encounters with muricid predators, was calculated as the number of unsuccessful drilling attempts divided by the total number of attempted drillholes (Vermeij et al., 1989) (Table 4). An effectiveness of 1.0 indicates that all drilling attempts by predators were unsuccessful, and conversely, an effectiveness of 0.0 indicates that the predator was always successful in encounters with its prey.

RESULTS AND DISCUSSION

Association between Predator and Prey Size

Principal components analysis: Muricid predator size is correlated with prey size. The loadings of the first eigenvector (56.0% of variation) of the correlation matrix between variables express covariation in the dimensions of

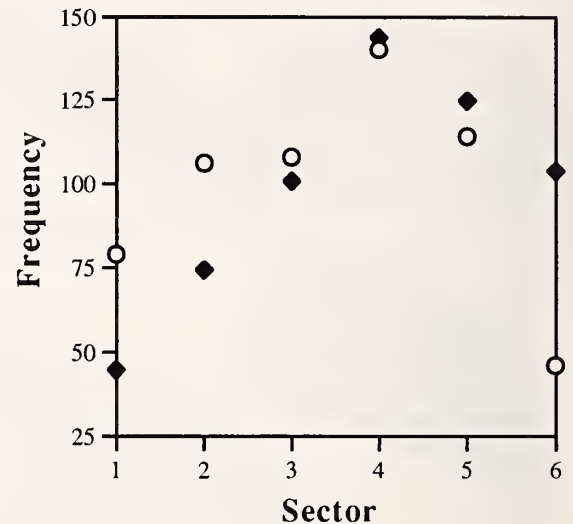


Figure 5

Plot of the observed (○) versus expected (◆) number of complete boreholes per sector. Expected frequencies calculated proportional to average surface area. A chi-square goodness of fit test results in a nonrandom distribution ($\chi^2 = 73.5$; $df = 5$; $P < 0.001$).

the drillhole (size of predator) and dimensions of the mussel valve (size of prey) (Table 1). The second eigenvector (35.7% of variation) expresses inverse variation in the dimensions of the mussel valve and drillhole.

The size of the predator and the size of the prey are correlated. However, the distribution of drillholes suggests a predation system in which the prey do not obtain a size refuge from predation (i.e., adult *N. lapillus* (OBD > 1.0 mm) successfully prey on a wide size range of adult mussels). In this case, all adult mussels would be vulnerable to *N. lapillus*. Similarly, Dayton (1971) reported that even shells of the thicker, *Mytilus californianus* Conrad, 1837, greater than 80 mm, were commonly found with complete muricid drillholes. However, only twenty-two (4%) of the mussels with complete boreholes were larger than 70 mm in A–P length (Figure 2). Mussels up to approximately 55 mm are preyed upon by a wide range of predators (0.7–2.0 mm OBD), whereas larger mussel size classes (60–70 mm) are drilled by a narrower size range of predators (1.5–2.0 mm OBD). This pattern suggests that generally mussels greater than 70 mm in A–P length obtain a size refuge from all but the largest drilling predators.

Linear regression: A comparison of the size selectivity between intertidal dogwhelk recruits (*sensu* early juveniles, Hughes et al., 1992), post recruits (smaller juveniles to subadults), and adults in interactions with *M. edulis* indicates a relaxation of selectivity in the subtidal adult muricid-mussel interaction. Hunt & Scheibling (1998) have shown that prey size is highly correlated with pred-

Table 2

Contingency table for locations of complete (C), incomplete (I), and repaired (R) boreholes according to six sector grid (see Figure 4); comparisons treated separately. Chi-square goodness of fit results in a nonrandom distribution of boreholes ($\chi^2 = 37.0$ and 35.6 ; $P < 0.001$ in both cases).

Sector	Observed frequencies		Total	Expected frequencies	
	C	I		C	I
<i>complete and incomplete</i>					
1	79	41	120	96	24
2	106	37	143	114	29
3	108	33	141	113	28
4	140	16	156	125	31
5	114	19	133	106	27
6	46	3	49	39	10
Total	593	149	742	593	149
<i>complete and repaired</i>	C	R		C	R
1	79	30	109	94	15
2	106	15	121	104	17
3	108	26	134	115	19
4	140	7	147	127	20
5	114	17	131	113	18
6	46	1	47	40	7
Total	593	96	689	593	96

ator size ($r^2 = 0.371$, $P = 0.001$) for early juvenile dogwhelks and that the coefficient of determination (proportion of the variation in predator size determined by variation in prey size) decreases ($r^2 = 0.254$, $P = 0.004$) in larger dogwhelk size classes (small juveniles to sub-adults). The adult dogwhelk-mussel interaction of this study also shows a significant correlation between OBD (of adult dogwhelks) and mussel shell length ($r^2 = 0.117$, $P < 0.001$) (Figure 3). Adult muricids successfully penetrated a wider range of mussel size classes than did younger cohorts of dogwhelks. Numerous mismatches evident from the least-squares regression of OBD on prey length (Figure 3) indicate that many undersized muricids successfully penetrated unpredictably large mussels. Similarly, Griffiths & Blaine (1994) reported a breakdown in the relationship between predator and prey size for *Nucella cingulata* (Linnaeus, 1771), preying on large (mean 52 mm A-P length) *Mytilus galloprovincialis* Lamarck, 1819, from the west coast of South Africa.

Constraint on size-selective foraging. A profitability curve, calculated as the ratio of predicted weight of tissue extracted to predicted handling times, for *N. lapillus* feeding on *M. edulis* is a monotonically increasing function of mussel shell length (up to 40 mm) (Hughes & Dunkin, 1984a). The profitability of mussels to *N. lapillus* declines as prey size increases beyond 40 mm, so that dogwhelks should selectively reject larger (> 40 mm) mussels encountered during foraging bouts (Hughes & Dunkin,

Table 3

G-test for goodness of fit of observed frequencies of complete, incomplete, and repaired boreholes to expected frequencies based on a Poisson distribution. Expected frequencies for complete boreholes calculated using a truncated Poisson distribution. Expected frequencies less than five were pooled with an adjacent class to obtain a joint class with an expected frequency greater than five. Observed frequencies were also grouped to match the grouping of expected frequencies to facilitate calculation of the G-statistic.

Number of boreholes per valve	Observed frequencies	Poisson expected frequencies	Significance
<i>Complete boreholes</i>			
0	—	—	
1	417	409.6	G = 4.91
2	66	77.1	Gadj = 4.90
3	11	9.7	df = 3 - 2 = 1
4	4	0.9	P < 0.05
Total	498	497.3	
<i>Incomplete boreholes</i>			
0	425	413.4	
1	97	115.3	G = 3.02
2	17	16.1	Gadj = 3.01
3	5	1.5	df = 3 - 2 = 1
4	2	0.1	P > 0.05
Total	546	546.4	
<i>Repaired boreholes</i>			
0	471	461.8	
1	62	78.0	G = 3.10
2	10	6.6	Gadj = 3.09
3	2	0.4	df = 3 - 2 = 1
4	1	0.02	P > 0.05
Total	546	546.8	

1984a). A correlation between predator and prey size is consistent with an energy-maximizing foraging strategy (Hughes & Burrows, 1990; Hughes et al., 1992). Dogwhelks are expected to select larger prey, the preferred size increasing with increasing predator size.

In the present study, however, the dogwhelk population may not have had the more profitable smaller (*sensu* intermediate of Hughes & Dunkin, 1984a) mussel size classes to prey selectively upon. Furthermore, adult dogwhelks are capable of successfully drilling a wide range of potential prey given sufficient time to complete the drilling process (evident from the low correlation between predator and prey size, $r^2 = 0.117$) (Figure 3). Thus the risk of attacking a larger mussel, which may be devalued by the predator because of the associated longer handling time, may have been unavoidable if more profitable prey size classes were unavailable or infrequently encountered. This foraging strategy was also documented for *N. cingulata* feeding on *M. galloprovincialis* by Griffiths & Blaine (1994). The most profitable prey when encoun-

Table 4

Prey effectiveness (PE) in deterring predation by drilling for *M. edulis* (PE = number of incomplete and repaired drillholes/total attempted drillholes). Overall PE = 0.29.

Size class (mm)	Complete	Incomplete	Repaired	PE
20–30	11	1	0	0.08
30–40	122	20	5	0.17
40–50	254	46	25	0.22
50–60	125	40	15	0.36
60–70	62	33	36	0.53
70–80	22	9	12	0.49
80–90	1	2	3	0.83
90–100	0	0	1	1.0

tered are selected, but if relative abundance or encounter rates with the most profitable prey are low, less profitable prey are selected by the predator (Hughes, 1980). Thus selective feeding of *N. lapillus* is constrained in mussel beds consisting of predominately large prey (> 40 mm).

Site Stereotypy in Positioning of the Borehole

Complete boreholes: Borehole site stereotypy is evident for *N. lapillus*, although all sectors host complete boreholes. Sectors 1 and 2, the umbonal regions of the shell, were preferentially drilled ($\chi^2 = 73.5$; $P < 0.001$) (Figures 1G, 5). Drillholes in sector six, the posterodorsal region of the valve (Figure 1J), were less frequent than expected based on the surface area of the sector (Figure 5).

Positioning of the borehole by the predator in the anterior region of the valve (sector 2) is consistent with the results obtained by Seed (1969) and Hughes & Dunkin (1984a). According to Seed (1969:340), placement of the borehole in the umbonal and posterodorsal regions is preferred, because "the shell is particularly thin and brittle either through excessive erosion (especially at the anterior end) or the absence of nacreous shell in the regions of muscle insertion (especially around the region of the posterior adductor muscle)." (See Figure 1F, for position of the anterior and posterior adductor muscles.)

Surprisingly, approximately fifty percent of complete boreholes in subtidal mussels were positioned in the ventral sectors of the valve (Table 3) (Figure 1B, C, G, J, K). Selection of ventral drilling sites is confounding because of the increased handling times associated with drilling through the thicker valve wall in this region of the shell (Hughes & Dunkin, 1984a). In contrast, Seed (1969:340) noted that complete drillholes were disproportionately concentrated on the dorsal portion of the valve of a sample of intertidal *M. edulis* (only an estimated 15% of drillholes occurred in ventral sectors). This contrast in the placement of the drillhole in mussel prey

by *N. lapillus* may reflect a trade-off between foraging and the risk of predation, due to differences in the abundance and diversity of exposed versus submerged dogwhelk predators.

To an individual dogwhelk the risk of predation may depend not only on the abundance of its predators, but also its own behavior. Foraging by the dogwhelk may increase the probability of mortality to predation (Gilliam, 1990). A shift in prey size-selectivity from large to small prey may reduce the time the forager is vulnerable, to predation, thus decreasing the probability of death to predation. Indeed, Palmer (1984) suggested that drilling muricid gastropods from the west coast of North America select small prey to reduce the risk of predation and other attendant risks of handling prey with long subjugation times. But, the predator-mediated shifts in prey size-selectivity may be constrained by the absence of smaller mussels.

Concentration of boreholes in the ventral sectors suggests a more inconspicuous drilling posture of the dogwhelk that is potentially less vulnerable to locally common crabs such as *Carcinus maenas* Linnaeus, 1758, and *Cancer irroratus* Say, 1817, (Elner, 1978; Hughes & Elner, 1979; Moody & Steneck, 1993), as opposed to being perched up and consequently more exposed on the dorsal margin of the shell. The risk of being attacked by molluscivores for *N. lapillus* may favor a suboptimal drilling site in the absence of alternative prey. The ventral drillhole location suggests a more cryptic drilling position that may provide a refuge from foraging predators during the increased handling times imposed by larger prey for *N. lapillus* in the absence of small mussels.

If dogwhelks preferentially drilled the thicker ventral sectors rather than the more easily penetrated dorsal regions of the shell to reduce the risk of being detected by predators, then the proportion of unsuccessful events should be higher in the dorsal sectors (due to an increased likelihood of disturbance). However, 67% of incomplete boreholes are located in the ventral sectors of the valve ($\chi^2 = 14.33$; $P < 0.001$). Moreover, 36 and 21% of all boreholes in the ventral and dorsal, respectively, portions of the valve are unsuccessful drilling events (either incomplete or repaired). This pattern seems inconsistent with the selection of a cryptic drilling site to reduce the risk of predation. But a more ventral drilling position, especially within sector 3 (Figure 4), also increases the likelihood that the drilling process will be interrupted by the adhesion of byssi by the mussel to the shell of the drilling predator (Davenport et al., 1996; Wayne, 1987). Interruption of the long drilling process of a snail positioned on the more exposed dorsal margin of the shell may result in death for the drilling predator (dogwhelks up to ~ 35 mm in shell height are vulnerable to crab predation; Hughes & Elner, 1979). In contrast, interruption of a snail drilling in the more cryptic ventral sectors

may only result in temporary entrapment in a mussel's byssus.

Incomplete boreholes: Both incomplete and repaired boreholes accumulated in the ventral umbonal sectors in greater frequencies than expected ($\chi^2 = 37.0$ and 35.6 , $P < 0.001$, respectively) (Table 2). The number of incomplete boreholes in umbonal sector 1 is nearly twice the expected number (41 versus 24) (Table 2). Repaired boreholes show a similar distribution for sector 1 (30 versus 15). The low numbers of both incomplete and repaired drillholes in the more posterior sector 4 relative to expected frequencies (Table 2) suggest that postero-anterior shifts influenced the observed distribution of unsuccessful events recorded on the shell at death. Unsuccessful attempts to drill the posterior margin of a young adult would leave an incomplete borehole that would occupy an increasingly more central and ultimately an anterior position late in ontogeny.

Relationship between Thickness of the Valve and Incomplete Boreholes

Carriker & Van Zandt (1972) have suggested that the muricid *Urosalpinx cinerea* (Say, 1822), selects a drilling site without regard to thickness of the shell (but see discussion by Hughes & Dunkin, 1984a for *N. lapillus* preying on mussels). Maximum depth of penetration is limited by the length of the fully extended proboscis of the predator. Proboscis length in *N. lapillus* approximates dogwhelk shell height (Hughes & Dunkin, 1984a). Given that shell thickness is phenotypically labile in *M. edulis*, being generally thicker in geographic areas of high predation pressure (Leonard et al., 1999), incomplete boreholes may represent a limit (i.e., thickness) to predation for *N. lapillus* feeding on large mussels.

Thickness of the mussel valve in the *Nucella-Mytilus* interaction did not limit predation for the size range of predators sampled (0.7–2.0 mm OBD). Valve thickness remains relatively thin, approximately 2.2 mm for even an 80 mm mussel in the umbonal region of the shell (estimated from regression equations given in Hughes & Dunkin, (1984a)). Moreover, based on shell thickness, any given size class of predator (> 1.0 mm OBD) was capable of drilling a mussel 70 mm in A–P length (Figure 3). Given an average drilling rate of 0.36 mm day⁻¹, for *N. lapillus* drilling *M. edulis*, a shell 2.0 mm thick would take about 5.5 days to penetrate (Hughes & Dunkin, 1984a). Thus incomplete boreholes most likely represent interruptions of the drilling process.

Frequency of Multiple Boreholes

Complete boreholes: The goodness-of-fit (G-test) of the observed frequencies to those expected by the Poisson distribution indicates that multiple complete boreholes (Figure 1H–J) occur in greater frequencies than predicted

($G_{adj} = 4.91$; $P < 0.05$) (Table 3). The clumped frequencies of complete boreholes in the tail of the distribution indicate that the occurrences of multiple boreholes on a single valve are not independent of each other. The occurrence of one successful drilling event enhances the probability of a second event occurring. Poisson probabilities of the occurrence of multiple complete boreholes on a single valve decrease as the number of complete boreholes on a valve increases (Figure 6), suggesting that multiply drilled valves are considerably rarer than singly drilled valves.

This clumping of multiple complete boreholes may occur due to the near synchronous initiation of the drilling process by conspecifics of *N. lapillus* on the same prey. Hughes & Dunkin (1984a) reported that only 60% of mussel tissue is extracted from 40 mm-long prey, i.e., the point of satiation for a given snail will occur before the entire mussel has been consumed. Thus, aggregations of conspecifics on the same mussel shell may continue the drilling process, penetrating the shell at different times (or simultaneously?).

The maximum number of snails that can mount and successfully drill the same mussel concurrently (producing multiple complete drillholes) may depend upon the interval of time between initiation of drilling by different snails. Brown & Alexander (1994) reported that the tenacity of *Stramonita haemastoma* (Gray, 1894), feeding on *Crassostrea virginica* (Gmelin, 1791), from the Gulf of Mexico was not dependent on the number of conspecifics that "joined" in the attack, but rather on the timing of the attacks. Multiple drillholes were observed in oyster valves, which suggested that most snails were attracted to the prey early and attempted to drill a hole. However, late-arriving snails may have abandoned unfinished drillholes to feed through the gaped valves. These snails were "cheating," sharing in the rewards but not the cost of foraging. The valves of *M. edulis* also gape after prolonged feeding of a drilling predator (Hughes & Dunkin, 1984a); thus it is reasonable to assume that some dogwhelks would abandon unfinished drillholes, although field observations are needed to substantiate this hypothesis. Similarly, Carriker & Van Zandt (1972:234) reported this behavior in *U. cinerea* feeding on *C. virginica* stating, "as feeding by the snail(s) continues, the adductor muscle of the oyster weakens and relaxes, and the valves begin to gape slightly"; subsequently, other conspecifics join in the attack by feeding through the gape between the valves.

However, it should be noted that the frequency of valves with multiple complete boreholes (Table 4) suggests that this behavior is either unlikely for or ineffectually practiced by *N. lapillus* feeding on large *M. edulis*, because as the first snail finished the drilling process, the other snails continued the slow process of excavating a drillhole, rather than adopting the more efficient "cheating" strategy. Studies are needed to determine how long

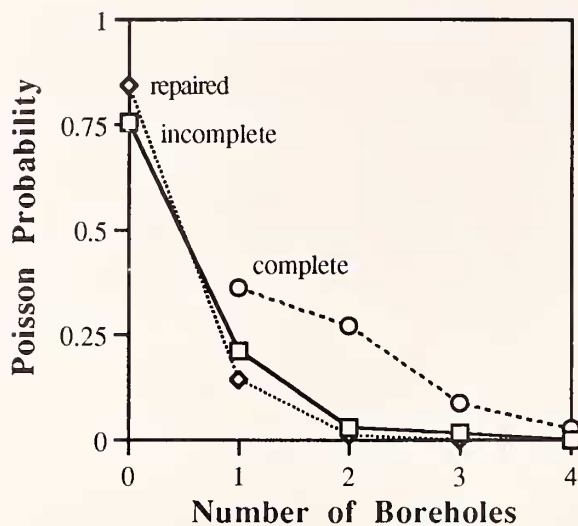


Figure 6

Plot of calculated Poisson probabilities of the occurrence of multiply complete (O), incomplete (□), and repaired (◇) boreholes in a single valve.

the valves of *M. edulis* remain adducted after the initial dogwhelk(s) penetrate the shell.

Repaired boreholes: The distribution of multiple repaired boreholes (Figure 1L), unlike the distribution of multiple complete boreholes, followed a Poisson distribution, indicating that the probability of surviving a successful penetration of the valve was independent ($G_{adj} = 3.09$; $P > 0.05$) of the number of encounters with drilling dogwhelks. Therefore, the majority of multiple repaired drillholes on a single valve can be inferred to have occurred independently of each other (i.e., resulting from successive attacks by individual predators rather than multiple snails drilling concurrently). Indeed, Griffiths & Blaine (1994) suggested that large *M. galloprovincialis* accumulate multiple sublethal attacks (predatory "cropping") by *N. cingulata* over time. Concurrent attacks by more than one snail would most likely result in the mussel's death. This ability to repair perforations in the shell away from the mantle edge shortly after dislodgement of the mounted predator is advantageous because any breach in the valve may allow chemical cues to attract other drilling snails, durophagous crabs, or asteriids (Vermeij, 1983; Carriker & Van Zandt, 1972; Elner, 1978; Hughes & Elner, 1979; Moody & Steneck, 1993; Reimer & Teddren, 1996), which are common subtidal coinhabitants. Indeed, the calculated Poisson probabilities (Figure 6) for the occurrence of multiple repaired drillholes are lower in comparison with probabilities for multiple complete and incomplete boreholes occurring on the same valve.

The repair of perforations in the shell of *M. edulis* requires up to 6 to 8 weeks in water temperatures of 18°C

(Meenakshi et al., 1973). (This slow experimental rate of repair may not reflect field conditions. Indeed, for 25–40 mm *M. edulis*, perforations < 2.0 mm in diameter are often repaired within a week in water temperatures of 21°C [R. R. Alexander, personal communication, 1999].) Consequently, there is considerable time for the injured mussel to be detected by predators such as *C. maenas* (Vermeij, 1983). The concentration of repaired drillholes in the larger size classes (mean mussel length = 59.4 and 47.9 mm for valves with repaired and complete boreholes, respectively, $t = 9.66$, $P < 0.0001$) may have been generated by the fact that at sizes greater than 50 mm in A–P length, mussels are effectively immune from attack by manipulative chelate predators such as *C. maenas* (Elner & Hughes, 1978; Seed & Hughes, 1995; Ameyaw-Akumfi & Hughes, 1987). Smaller mussels may physiologically be able to repair perforations in the shell, but because they are in the size range vulnerable to foraging crabs, they are more prone to attack during the prolonged repair phase, and therefore less likely to show repaired injuries. Indeed, Seed (1969), working with intertidal mussels < 50 mm in A–P length, rarely encountered repaired drillholes. In this study, only 5.2% of the total number of repaired boreholes were apportioned in the 20–40 mm size classes (Table 4). Similarly, no repaired drillholes were found in shells of *M. galloprovincialis* less than 40 mm (Griffiths & Blaine, 1994). Alternatively, Griffiths & Blaine (1994:fig. 3; p. 348) have suggested that there is a critical ratio of prey size to predator size above which prey survivorship is high in predator-prey interactions involving *N. cingulata* and *M. galloprovincialis*. Below this threshold, prey were almost always killed and completely consumed.

Prey Effectiveness in Detering Drilling Predators

Effectiveness and adaptation: The effectiveness of an individual in a given environment is the probability that the individual survives in an encounter with a potentially lethal hazard, e.g., a predator (Vermeij, 1982a). An effectiveness of 0.0 suggests that the predator was always successful. To recognize a character or behavior that confers an adaptive advantage, individuals must survive in encounters with predators (Vermeij, 1982a).

Prey effectiveness (PE) in deterring drilling muricid gastropods was 0.29. Vermeij et al. (1989) reported a value of 0.17 for a geographically proximal sample from Sheep Island, off Deer Isle, Maine. Prey effectiveness estimates increase as shell size increases (Table 4). This pattern suggests that dogwhelks were less efficient in dealing with increasingly larger and thicker shells. However, the accumulation of unsuccessful drilling attempts with size most likely reflects an increased probability of encountering drilling muricids over the lifespan of an individual. Indeed, the distribution of multiple incomplete boreholes followed a Poisson distribution indicating that

the majority of incomplete boreholes occurred independently of each other as the result of successive attacks by individual predators (Table 3). Clearly, as the lifespan of the mussel increases, the likelihood of encountering a drilling predator also increases.

From the point of view of the surviving prey there may not be a difference between an incomplete and a repaired drillhole (G. J. Vermeij, personal communication 1998), i.e., the mussel survived both the drilling event that culminated in an incomplete borehole and that which produced a complete hole that was later repaired. The ability to repair complete boreholes, however, may be a physiological adaptation that increases the survivorship of the prey. Repaired boreholes represent survival of the subjugation phase of a predation event, a necessary condition for the recognition of adaptations that confer benefits with respect to survival (Vermeij, 1982).

Whether or not the cessation of the drilling (subjugation) phase of predation was due to interruption of the esurient predator by extrinsic biotic or abiotic factors, or to an intrinsic active defensive behavioral response of the mussel, is not known. Dogwhelks are actively entrapped by adhesion of byssi to the snail's shell, which usually only temporarily immobilizes the snail (Davenport et al., 1996; Wayne, 1987; Carriker, 1981). In addition, Wayne (1987) has described behavioral interactions between *M. edulis* and *Nucella emarginata* (Deshayes, 1839), and *Nucella lamellosa* (Gmelin, 1791). After initial contact with the dogwhelk, the mussel's valves alternately gaped widely (retracting the mantle) and closed (this behavior may pinch the muricid's foot causing it to move away from the valve edges). Indeed, only a few valves had complete boreholes near the valve margins (Figure 1J). Furthermore, large mussels may be able to dislodge mounted snails by a sweeping motion of the narrow, fingerlike foot. Wayne (1987) described a similar action of the foot as "probing and wiping." Contact with the mussel's foot elicited a "lifting and twisting" behavior in the dogwhelk, as well as directed retaliatory rasps at the foot of the mussel with the radula (see Wayne, 1987:fig. 1, p. 141).

The ability to repair drillholes is an adaptation that complements the high probability of disturbance of drilling predators in this shallow-subtidal habitat. Sealing off a perforation in the valve would decrease the probability of detection by other predators, thus increasing survivorship. The variegated behavioral defenses (as well as inducible morphological defenses; i.e., thickness (Leonard et al., 1999)) of *M. edulis* function to increase the likelihood of successfully deterring attacks by specialized predators (i.e., drilling muricids), thus increasing fitness by reducing the risk of predation. The valve flapping movements, flailing foot extensions, and byssus attachment by *M. edulis* described by Wayne (1987) not only act to deter drilling predators upon initial contact, but may also increase the chances of disturbing muricids that

have penetrated the interior of the shell with the extensible proboscis. Studies documenting the effectiveness of mytilids in different phases of predation by drilling muricid predators are needed to independently test whether the inferred defensive adaptations of extant species have evolved specifically in response to drilling muricids. Are active behavioral defenses more successful after the predator completes the drillhole?

Bias in prey effectiveness?: If *N. lapillus* actively abandons an unfinished drillhole in favor of feeding through the gaping valves in prey that had already been successfully penetrated by conspecifics, then PE estimates may overestimate the defensive value of the mussel's shell. One hundred valves in the sample contain both complete and incomplete boreholes. Incomplete boreholes found in association with complete boreholes may either represent a "true" unsuccessful drilling attempt most likely due to interruption of the prolonged drilling process of large *M. edulis*, or, alternatively, an incomplete borehole may represent a muricid that "cheated" and abandoned a drillhole in foraging bouts where snails initiate the drilling process concurrently. The latter situation will artificially inflate the PE estimate. The predatory attack of several snails (*sensu* group foraging of Brown & Alexander, 1994) may result in multiple complete and incomplete boreholes in the prey's valve. In these cases, however, the mussel did not survive the attack even though the shell recorded the abandoned incomplete drillhole as an unsuccessful drilling event. In contrast, repaired drillholes and valves with only incomplete drillhole(s) represent unquestionable survival of an unsuccessful drilling event. Only 47 (8.6%) valves had evidence of unsuccessful (incomplete and repaired) drilling events recorded on the valve not in association with the successful events.

Another important caveat to the estimation of PE in deterring muricid drilling predators is the possibility of the recognition and reoccupation of failed drilling attempts by other muricid conspecifics. Resumed drilling of a formerly incomplete borehole not only decreases the handling time of the prey, but also the calculated PE estimate. Reoccupying incomplete boreholes will decrease the number of unsuccessful drilling events recorded on the shell (decreasing the numerator in the PE ratio); thus PE estimates may also be slightly underestimated. This behavior of reselecting formerly initiated drillholes has been documented for *N. lapillus* feeding on *M. edulis* (Hughes & Dunkin, 1984a).

Concluding Remark

This study illustrates how much is still not known about the predator-prey relationship between *N. lapillus* and large size classes of *M. edulis*. Clearly, there is a need for experimental work to determine the cost and benefits of the reconstructed foraging behaviors of *N. lapillus* feeding on large mussels when the preferred smaller prey

size classes are rare or absent. Constraints on foraging may include the increased probability of mortality to predation with increased handling time of large prey and active behavioral defenses of the prey which disrupt the drilling process. Alternative predatory strategies (i.e., selecting a ventral drilling position, group foraging, and predatory "cropping"?) that exploit large prey with increased handling times are also observed in other predator-mussel interactions (see Ameyaw-Akumfi & Hughes [1987]). Similar foraging "rules" may also apply for the adult *N. lapillus*-*M. edulis* predator-prey interaction.

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